

MORPHO-FUNCTIONAL ANALYSIS OF THE JAW APPARATUS OF SOUTHEAST ASIAN TROPICAL FOREST TIMALIID BIRDS

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ABSTRACT

The biology of many forest birds of Southeast Asia is still poorly known, and requires extensive field study. An original method of morpho-functional analysis of the jaw apparatus, used in our research, has proven to be extremely useful in this area. This methodology helps to interpret data from the field, as well as to hypothesize certain features of timaliid feeding biology without direct field observations. Our method includes a detailed description of the morphology of the jaw apparatus, with a subsequent biomechanical analysis of its mechanical properties allowing the investigation of the possible evolution of trophic adaptations in selected species. A comparison of several congeneric species provides insight into the feeding adaptations within a genus and – on an even broader scale – within a family. Our data can be used for the prediction of the ecological niches of species and their preferred habitat types, as well as their possible reactions to major changes in the habitat. Here we present some results of our method as applied to seven timaliid species inhabiting the lowland forests of Vietnam.

Key words: Forest bird biology, morpho-functional analysis, jaw apparatus, biomechanics, Timaliidae, Vietnam.

INTRODUCTION

The ecology of tropical forests has been a major focus in recent biological research. One of the most important aspects of such research has been trophic interactions. The feeding adaptations of birds are of particular importance, given the high level of avian metabolic rates. Peculiarities of these adaptations in passerines have been a core objective of my field surveys in Vietnam, which started in 1989 (Kalyakin 2008). The chief aim of this work was to outline specific features in the biology of tropical passerines as key points for understanding the functioning of tropical forest ecosystems. This focus was part of a broader program carried out by the Joint Russian-Vietnamese Tropical and Research Centre, whose goal is the investigation of the diversity, structure, and function of the tropical forest ecosystems of Vietnam as a basis for their protection and sustainable development. Here I present the part of those studies that relate to trophic adaptation in lowland forest timaliids of Vietnam.

I define “trophic adaptations” as a complex of specific morphological, functional, behavioral, and ecological features necessary for the effective processing of food (locating, capture, manipulation, swallowing, etc.). The main themes of this paper are the structure and functional characteristics of the jaw apparatus and their relation to birds’ everyday life.

The functional analysis of the avian jaw apparatus has been a popular topic since the middle of the last century. Studies by Beecher, Bock, and Zusi are among the best known. However, the main input in the topic was made by Soviet morphologists. Konstantin A. Judin outlined the basics of the morpho-functional analysis of avian jaw apparatus (Judin 1957, 1965, 1970). Felix Ya. Dzerzhinsky developed his ideas, applying them to the analysis of various groups of birds (e.g., Dzerzhinsky 1972, 1977, 1980, 1982, 1997). The method used for morphological studies of the jaw apparatus was developed by Dzerzhinsky (e.g., 1997), and allows a decoding of the mechanical properties of the bill structure.

Passerines are quite suitable for morphological research. Their overall small bill size (except for corvids), along with a high degree of uniformity in the jaw apparatus (Beecher 1953, Kalyakin 2002, 2008), make it possible to select several so-called morphological 'syndromes' (more than one feature) (Dzerzhinsky 1997). These can be used for the analysis of each individual jaw apparatus. For example, flycatching presumes a well-developed lig. postorbitale, together with a light, thin lower jaw, and long-fibered muscles with simple inner aponeurotic carcasses. Frugivory, in turn, requires long-fibered muscles and reinforcement of the upper jaw against passive protraction – enlargement of muscles (chief among them m. retractor palatini), development of new muscular heads, and a special construction of the maxillary joint (Kalyakin 2002, 2003). The adaptation to fix the maxillary joint develops if strong pressure in the bill is necessary to catch large and/or mobile prey. Stronger pressure is also achieved by enlarged jaw muscles with a complex inner structure (the pinnate muscles of laniids and corvids: Dzerzhinsky & Mottowj 1989).

This method of morpho-functional analysis has been successfully applied by F. Dzerzhinsky (see above) and L. Korzoun with co-authors to many non-passerines (Korzun 1978, 1986, 1994, 1996, 1998; Korzoun 1991; Korzun & Trunov 1997; Korzoun *et al.* 2003). Some families of passerines were also included in the scope of their studies (Dzerzhinsky & Yesilevskaya 1986, Dzerzhinsky & Mottowj 1989, Korzoun *et al.* 2000). My own research started with the study of 16 species of SE-Asian bulbuls (Pycnonotidae) (Kalyakin 1998, 2002, 2003) and later, in the course of preparation for my doctoral thesis, incorporated species from 15 other families (Kalyakin 2007a, b; 2008, Kalyakin & Korzoun 2007). Among the wide spectrum of species, and aspects of ecology, and morphology which are discussed in my thesis, timaliids were represented by 11 species in 11 genera. Seven of them inhabit the lowland forests of southern Vietnam. In discussing the morpho-functional peculiarities of their jaw apparatus, data on other species were used, namely that on bulbuls and on one or two species from each of 15 other families.

The main result of the morpho-functional method is an understanding of how a particular jaw apparatus functions and what kind of movements it performs with high, medium, or low effectiveness. This allows us to identify peculiarities in a particular

apparatus in its evolutionary development, which brings us close to the reconstruction of real phylogeny. For example, analysis shows that laughingthrushes are members of family Timaliidae, which are, in turn, closely related to parrotbills, regardless of their modern systematic position. The comparison between closely related groups enhances the precision of the approach, refining our knowledge on ecological niches of particular species in stable or changing environment. It is unnecessary to say how important this is for the protection of species and their environment, especially in rapidly vanishing tropical forest ecosystems.

METHODS

Field studies of timaliid trophic behavior were supplemented by investigations into the morphology and biomechanics of their jaw apparatus. The dissections were carried out in the Zoological Museum and Vertebrate Zoology Department of Moscow Lomonosov State University under the kind supervision of Felix Ya. Dzerzhinsky and Leonid P. Korzoun.

Field studies began in 1989, and were organized as a series of short-term visits to several forested areas of Vietnam. The first three years of the studies were dedicated to the investigation of bird ecology in Ma Da Forest Enterprise in southern Vietnam (see below). Later trips involved visits to many different parts of the country. Field observations were made on plots, along transects, or near fruiting trees, as well as by checking the stomach contents of collected birds. Each field record contained time of observation, locality, habitat, foraging height, number of individuals, and description of their activities (including feeding behavior). These studies brought rich material on the diversity of avian communities, individual trophic niches, and other aspects of biology for many birds of Vietnam (Kalyakin 1995, 2006a, 2007b; Kalyakin *et al.* 1997; Kalyakin & Korzun 1998, 2001). More than 2000 observations were recorded for timaliid species. They were subsequently used for descriptions of their biology (see below).

Most of the field work was done at two sites – Ma Da Forest Enterprise (11°20'N, 107°00'E) and Cat Tien National Park (11°27'N, 107°18'E), both in Dongnai Province, 55 and 80 kms NE of Ho Chi Minh City (Fig. 1). Despite differing tree composition, both localities have one aspect in common – they were logged at roughly the same time, 30–40 years ago. The logging focused on selective extraction

of valuable timber belonging to the families Dipterocarpaceae, Fabaceae, and several others. The Ma Da forest, where investigations were carried out during 1989–1994, is a secondary lowland dipterocarp forest, with *Dipterocarpus dyeri* serving as a dominant canopy species. Average altitude is c. 100 m above sea level; climate is monsoon with a rainy season that lasts from May to October–November. Data on timaliid species were also collected in Cat Tien National Park based on two short visits in 1990 and 1994, and longer ones in 2002, 2003, 2006, 2008, and 2009 (4 months in total). The main habitat studied here was a Lagerströemia forest, a habitat in which the dominant tree species include *Lagerströemia*, *Tetrameles nudiflora*, *Azelia xylocarpa*, among others) and characterized by some disturbance by logging, a largely closed canopy, and considerable undergrowth. Different kinds of open habitat were

also visited including shrubby, treeless habitats with some bamboo. Other characteristics are similar to those for Ma Da forest except periodical flooding of part of its territory.

Field observations of avian behavior, especially those in complex ecosystems such as tropical forests, are not always effective due to the absence of knowledge of the functioning of locomotor and feeding apparatus. The required knowledge can be obtained only through morphological studies. These studies are very sensitive to the minute changes in trophic adaptations as well as to their history. Morphological studies were done together with field observations. Based on the meticulous dissections of the jaw apparatus (Figs. 2 & 3), the method of functional analysis of the jaw apparatus incorporates the biomechanical analysis of a free-body diagram. Forces (represented by vectors) acting on the food item pressed in the tip of the bill

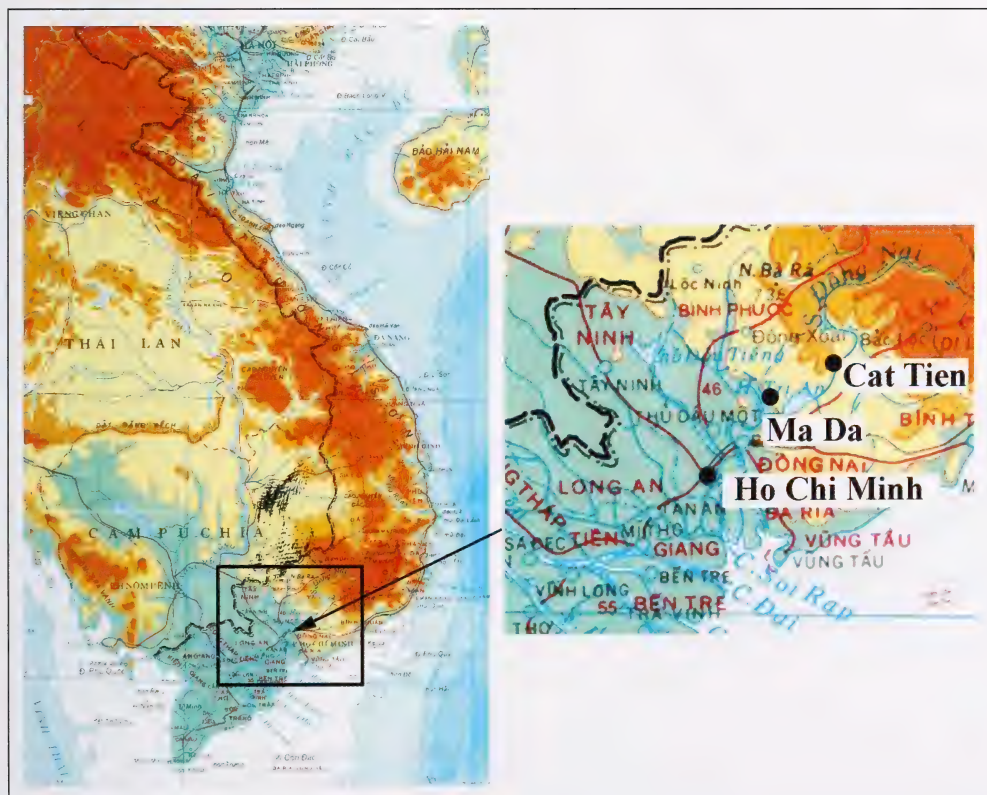


FIG. 1. Locations of study areas in southern Vietnam.

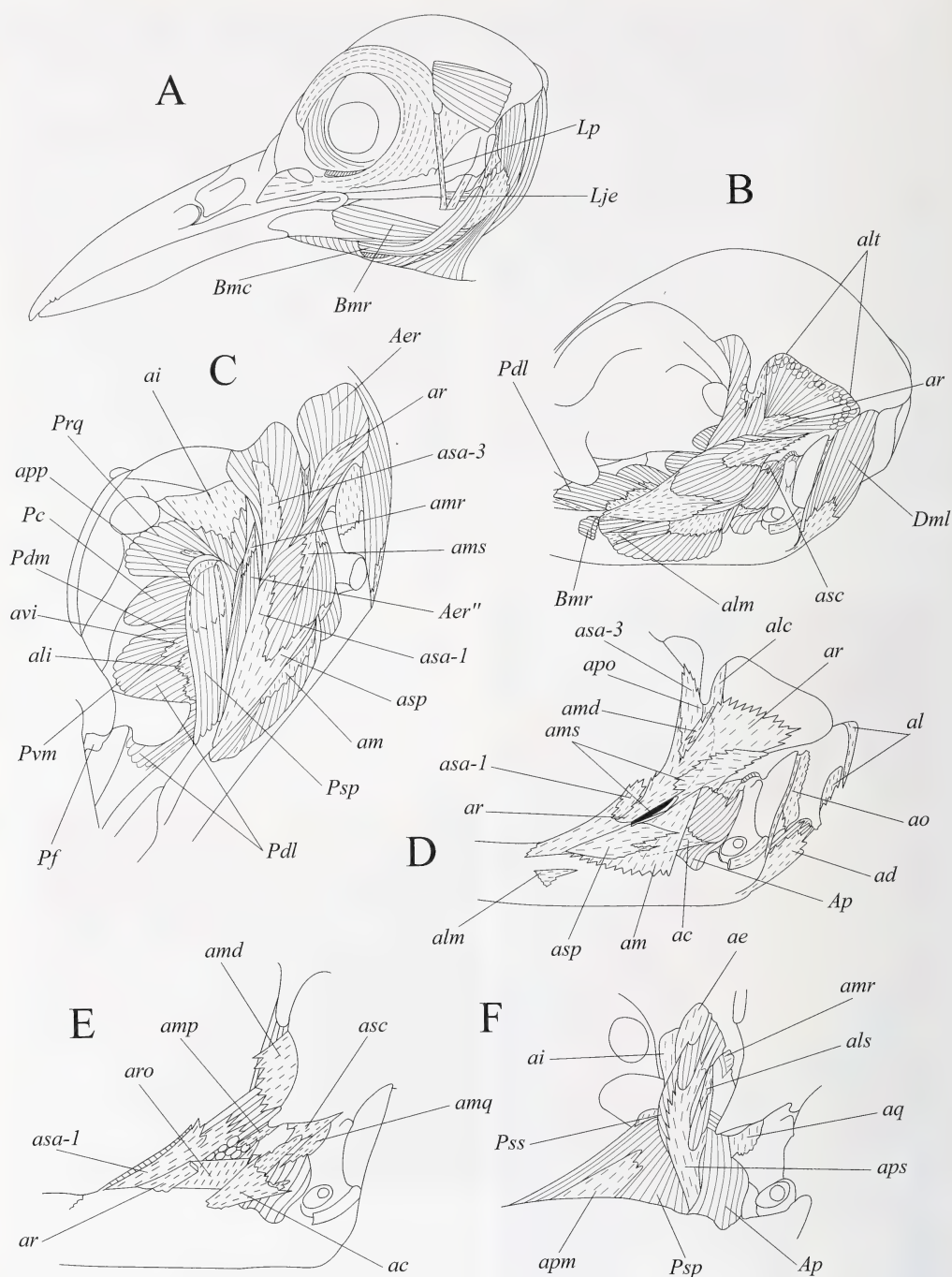


FIG. 2. Morphology of the jaw apparatus of White-crested Laughingthrush *Garrulax leucolophus*: jaw muscles and ligaments; side view; A-F – successive stages of dissection. See Comments in Attachment.

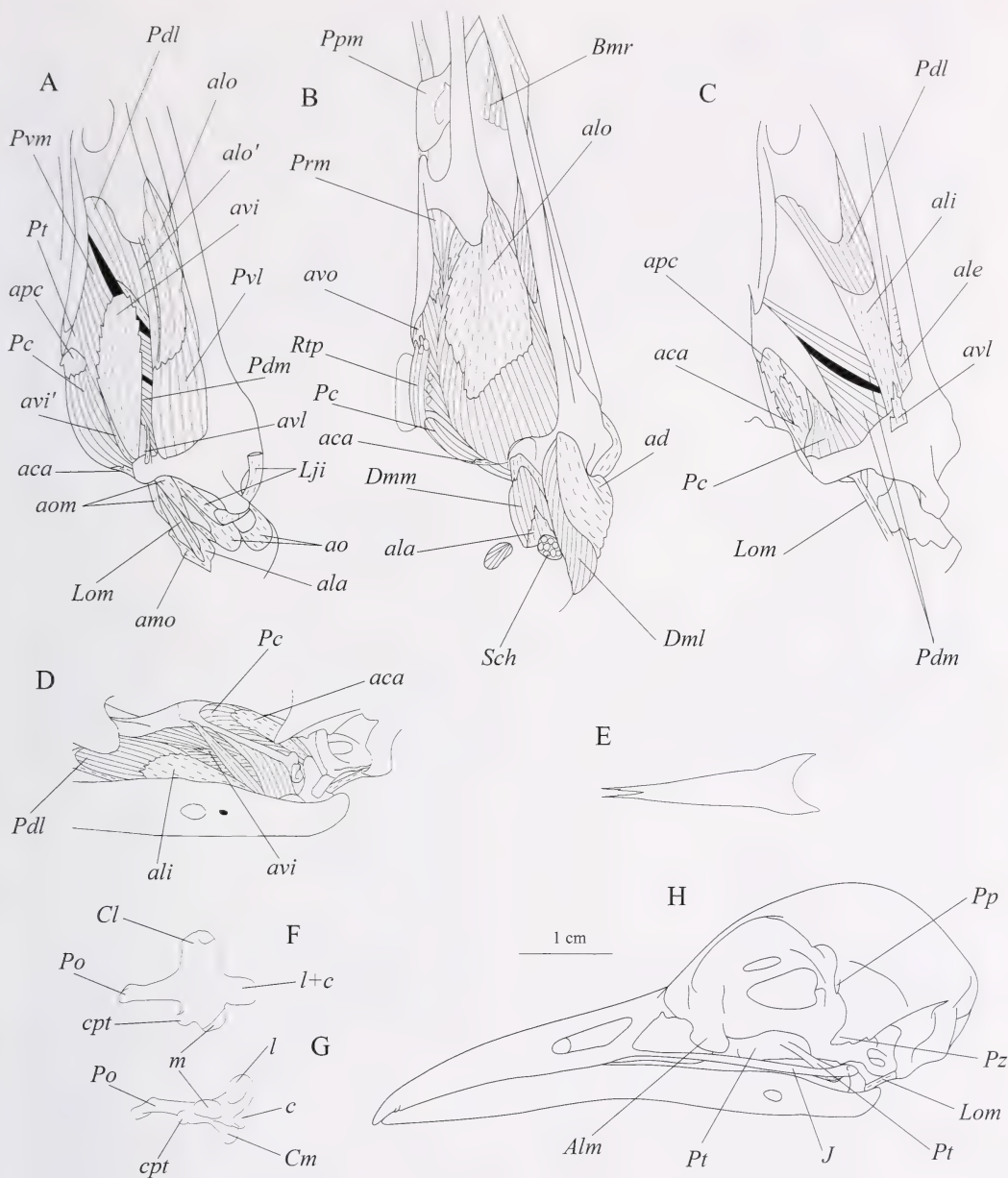


FIG. 3. Morphology of the jaw apparatus of White-crested Laughingthrush *Garrulax leucolophus*: A-C – portions of m. pterygoideus, several other muscles, ligaments, and elements of the skull; view from below; successive stages of dissection; D – m. pterygoideus, side view after removal of os quadratum; E – tongue; F – os quadratum, lateral view; G – os quadratum, view from below; H – skull, lateral view. See Comments in Attachment.

ATTACHMENT

Legend to the Figures 2 and 3:

Aponeuroses of muscles (*aponeurosis*):

ac – ap. caudalis
aca – ap. accessoria
ad – ap. depressoris
ai – ap. interna
al – ap. lambdoidea
ala – ap. lateralis
ale – ap. lateralis externus
ali – ap. lateralis insertionis
alo, alo' – ap. lateralis originalis
als – ap. lateralis superficialis
alt – ap. lateralis temporalis
alm – ap. lateralis medialis
am – ap. medialis
amd – ap. medialis dorsalis
amo – ap. mandibulooccipitalis
amp – ap. medialis posterior
amq – ap. medioquadrata
amr – ap. mediorostralis
ams – ap. mediosuperficialis
ao – ap. occipitalis
aom – ap. occipitomandibularis
apc – ap. pterygoidea caudalis
apo – ap. postorbitalis
app – ap. pseudotemporalis profundus
aps – ap. pseudotemporalis superficialis
aq – ap. quadrata
ar – ap. rostralis
aro – ap. rostralis originalis
asa-1, asa-3 – ap. superficialis anterior
asc – ap. superficialis caudalis
asp – ap. superficialis posterior
avi, avi' – ap. ventralis insertionis
avl – ap. ventralis lateralis
avo – ap. ventralis originalis

Muscles (*musculus*):

Aer, Aer' – m. adductor mandibulae externus,
 pars rostralis and pars medialis
Ap – m. adductor mandibulae posterior
Bmr – m. branchyomandibularis rostralis
Bmc – m. branchyomandibularis caudalis
Dml – m. depressor mandibulae pars lateralis
Dmm – m. depressor mandibulae pars medialis
Pc – m. pterygoideus caudalis
Pdl – m. pterygoideus dorsalis lateralis
Pdm – m. pterygoideus pars dorsalis medialis
Prq – m. protractor quadrati
Psp – m. pseudotemporalis profundus
Pss – m. pseudotemporalis superficialis
Pvl – m. pterygoideus pars ventralis lateralis
Pvm – m. pterygoideus pars ventralis medialis
Rtp – m. retractor palatini
Sch – m. stylohyoideus

Ligaments (*ligamentum*):

Lje – lig. jugomandibulare externum
Lji – lig. jugomandibulare internum
Lom – lig. occipitomandibulare
Lp – lig. postorbitale

Elements of the skeleton:

Alm – ala mesethmoidalis
c – condylus caudalis
Cl – condylus lateralis processu otici
Cm – condylus medialis processu otici
cpt – condylus pterygoideus
J – jugale, arcus jugalis
l – condylus lateralis
l+c – condylus lateralis + condylus caudalis
m – condylus medialis
Pf – praefrontale
Po – processus orbitalis quadrati
Pp – processus postorbitalis
Ppm – processus palatinus maxillaris
Pt – pterygoideum
Pz – processus zygomaticus

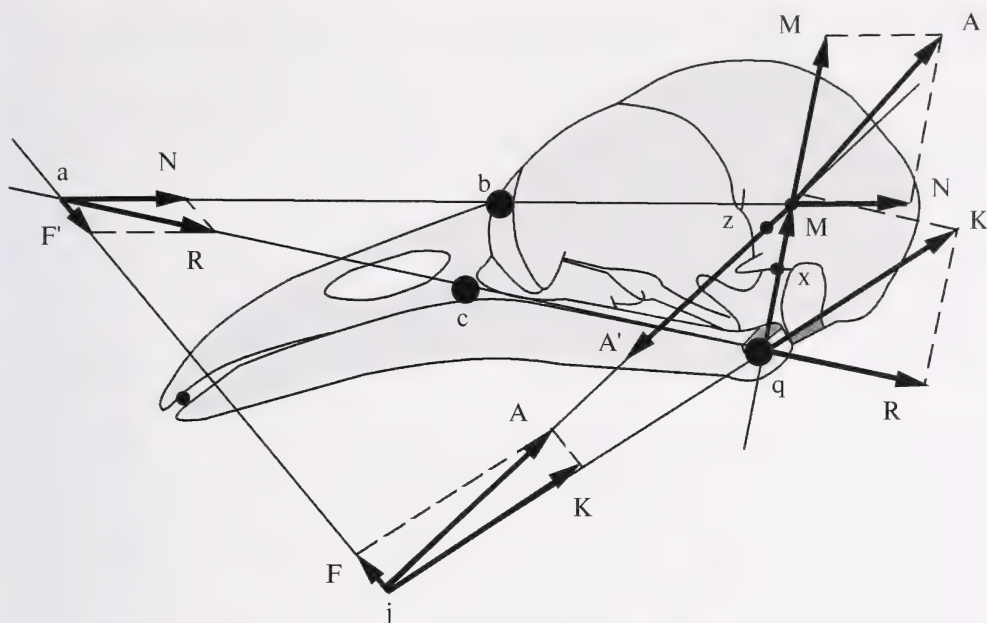


FIG. 4. Free-body diagram of forces acting in the skull during pressure on the small food item (small black dot) near the tip of the bill (after Dzerzhinsky 1972); the jaws are under independent muscle control. A – resulting force of dorsal adductors; F, K, N, M and R – forces of selected jaw muscles in an interaction with the food item reaction force; c – point of application of m. pterygoideus force to the upper jaw; x – rotation point of os quadratum against the skull; q – rotation point of lower jaw; b – rotation point at the base of the upper jaw; aj – line of action of forces pressing the food item; z – intersection point of lines ab and qx.

are analyzed (Fig. 4). The rotation of individual elements around each other allows identification of the role of each bone, muscle, and ligament in the processing of food items (Dzerzhinsky, 1972).

RESULTS

Ecology of timaliid species

An overview of the ecology and behavior of timaliids from southern Vietnam is necessary in order to interpret the morphological material. The following information is based on the study of a 20-ha plot in Ma Da Enterprise (Kalyakin *et al.* 1997). The composition and structure of the avian community of Ma Da are more closely related to those in Malaysia than to any others in central or northern Vietnam known to me.

There are 12 species in 8 genera of timaliid birds in southern Vietnam. The Chestnut-capped Babbler *Timalia pileata* is excluded from the list as an inhabitant of open grasslands. Eleven species of 7 genera were recorded in Ma Da. Abbott's Babbler *Malaccincincla abbotti* was not observed; however it was found in considerable numbers in Cat Tien National Park. Out of the total of 163 species of birds recorded in the study plot in Ma Da, the 11 species of timaliids comprise 6.7%. This percentage is less than is found in several other forested areas of Vietnam, located at higher altitudes, or in more northern regions of the country. Ten timaliid species were resident on the plot, while the Black-throated Laughingthrush *Garrulax chinensis* was a vagrant (Table 1).

TABLE 1. Biological features of forest timaliid species on the study plot in Ma Da forest, Dongnai Province, Vietnam.

Species	Abundance	Habitat	Stories in forest vegetation	Trophic links	Participation in mixed flocks
White-bellied Yuhina <i>Erpornis zantholeuca</i>	Rather common	Forest and forest edges, prefer closed-canopy forest	Canopies	Insects	Periodically
Black-browed Fulvetta <i>Alcippe grotei</i>	Common	Forest edges	Understory	Insects, small fruits	Stable
Great Scimitar Babbler <i>Pomatorhinus hypoleucos</i>	Uncommon	Forest and forest edges	Ground, understory	Insects	Rare
Striped Tit Babbler <i>Macronous gularis</i>	Abundant	Forest edges	Understory	Insects, occasionally small fruits	Periodically
Grey-faced Tit Babbler <i>Macronous kelleyi</i>	Abundant	Forest and forest edges	Understory, canopies	Insects	Stable
Buff-breasted Babbler <i>Pellorneum tickelli</i>	Common	Forest and forest edges	Ground, understory	Insects	Rare
Puff-throated Babbler <i>Pellorneum ruficeps</i>	Rather common	Forest and forest edges	Ground	Insects	Rare
Scaly-crowned Babbler <i>Malacopteron cinereum</i>	Abundant	Closed-canopy forest	Understory	Insects	No
White-crested Laughingthrush <i>Garrulax leucolophus</i>	Very abundant	Forest and forest edges	Ground, understory	Insects, occasionally fruits	Stable
Lesser Necklaced Laughingthrush <i>Garrulax monileger</i>	Uncommon	Forest edges	Ground, understory	Insects, possibly small fruits	Stable

Abundance

Most of the timaliid species had rather high population densities in the plot. The White-crested Laughingthrush *Garrulax leucolophus* absolutely dominated – c. 100 individuals per sq. km – being the most numerous among local species. Playing an important role in forest ecosystems, this laughingthrush is numerous due to the rich forest floor of *Dipterocarpus dyeri* leaves and dense understory as a result of selective logging.

Three other timaliids were among the most abundant birds in a study plot. They are Scaly-crowned Babbler *Malacopteron cinereum*, Grey-faced Tit Babbler *Macronous kelleyi*, and Striped Tit Babbler *Macronous gularis* with around 50 individuals per sq. km. Two species, Black-browed Fulvetta *Alcippe grotei* and Buff-breasted Babbler *Pellorneum tickelli*, were slightly less abundant with 40–50 individuals per sq. km. Thus more than half of the timaliid species can be considered as common and very common for the local forest avian community.

White-bellied Yuhina *Erpornis zantholeuca* and Puff-throated Babbler *Pellorneum ruficeps* were also common. The low density was recorded only for Lesser Necklaced Laughingthrush *Garrulax monileger* and Great Scimitar Babbler *Pomatorhinus hypoleucos*.

Habitats

Most of the above-mentioned birds belong to truly forest species, except for Striped Tit Babbler, which inhabits forest edges, and Black-browed Fulvetta plus Lesser Necklaced Laughingthrush, which avoid high forests. Almost all the species, though, can be occasionally observed along the edges of high forest (clearings, roads and paths, partially opened forested areas). Only Scaly-crowned Babbler seems to be confined strictly to the areas of closed-canopy forest; Large Scimitar Babbler and White-bellied Yuhina also show preferences for such habitat type.

Occupation of different stories of forest vegetation

Confinement to certain stories is a very important parameter of ecology of forest species due to the

pronounced differences there in temperature, light, and humidity. Timaliids inhabit almost all the forest stories except for the highest ones; they are only rarely recorded in the crowns and canopies of emergents. Only White-bellied Yuhina periodically collects food in lower parts of canopy formed by emergents. The lower we travel the more species of timaliids we meet. Puff-throated Babbler, Buff-breasted Babbler, and Large Scimitar Babbler, as well as two species of laughingthrushes *Garrulax* spp. can be treated as ground birds, partly exploiting lower stories. Scaly-crowned Babbler can also be seen foraging on the ground. Lower parts of emergent crowns are used by White-bellied Yuhina and Grey-faced Tit Babbler, while the understory at various levels is exploited by most of the species mentioned plus Black-browed Fulvetta. Primarily lower stories are occupied by White-crested Laughingthrush, Lesser Necklaced Laughingthrush, Scaly-crowned Babbler, and Striped Tit Babbler.

Trophic links

Timaliid species of lowland forests of southern Vietnam are mainly insectivorous: six species feed only on invertebrates, three others are predominantly insectivorous (see below). Obligate frugivory is reported for Black-browed Fulvetta, which in addition to insects and spiders feeds on fruit pulp. White-crested Laughingthrush, Lesser Necklaced Laughingthrush, and Striped Tit Babbler only occasionally exploit fruits, being facultatively frugivorous birds. Many of the timaliid species of lowland forest of southern Vietnam frequently participate in so-called mixed flocks of insectivorous birds. This is true for all the forest species except for Buff-breasted Babbler and Abbott's Babbler (in Cat Tien Park). The babblers in this study are only rarely seen feeding on the ground or in lower stories in or near mixed flocks. White-crested Laughingthrush, Grey-faced Tit Babbler, and Black-browed Fulvetta seem to be the organizers of such flocks. Scaly-crowned Babbler forms flocks of its own, in which several species of small insectivorous birds only rarely participate. The question of mixed flock formation and the role of timaliids in this process are matters dealt with in a separate study.

Thus forest timaliids of southern Vietnam comprise a group of breeding resident species of small and medium-sized birds, which are more or less abundant and, being predominantly insectivorous, exploit lower stories and forest edges. Only one species can

be considered truly frugivorous, while three others can be placed in the subgroup of facultatively frugivorous birds.

Results of morpho-functional analysis and discussion

Morphology and principles of the functioning of the jaw apparatus in the Timaliidae are similar to those in other passerines studied (Figs. 2, 3, 5, 6 & 7). It is adapted to picking a food item by the tip of the bill with subsequent manipulations by the coordinated efforts of muscles, which move the upper and lower jaws. In timaliids, as in other oscines, this coordination is achieved mainly by external adductors and *m. pterygoideus* (Fig. 4).

Despite the general similarity to other oscines, the timaliid jaw apparatus shows some peculiarities. Among them are the small or very small condylus caudalis of quadrate bone and long tiny *lig. jugomandibulare externum* (Fig. 2 & 3). These features, along with the weakness of *lig. postorbitale* indicate the possibility of a simultaneous movement of the jaws when the bill is closed or slightly opened. This is an adaptation for searching in substrate or picking and processing food with a closed or slightly opened bill; an ability to make short vertical and longitudinal movements which help to break up food items.

The other interesting features found in Timaliidae, including parrotbills, is an ability to see food or the substrate close in front of the bill, or even at its tip. All these birds possess very small lateral wings of *mesethmoideum* (Figs. 2, 3, 5, 6, & 7), which usually obscure the field in front of the birds' eyes. This feature, characteristic of Timaliidae and parrotbills, is also described for Sturnidae and Icteridae (Beecher 1951, 1978, Dzerzhinsky 1997). It is considered to be an adaptation for food manipulation in the bill.

The third feature of the jaw apparatus which characterizes its properties is the volume and complexity of the inner structure of the jaw muscles. Timaliidae are in this respect somewhere in the middle among the oscines, being far behind the corvids and laniids. However, there is one lineage in the Timaliidae which shows a trend to reinforcement of jaw musculature. It includes Large Scimitar Babbler and Grey-Headed Parrotbill *Paradoxornis gularis* (Fig. 6). Similar in general, the reinforcements in these two species differ in details due to the difference in bill shape. The reinforcement is necessary to break open the substrate and excavate food items. This habit is observed in parrotbills and was found in several species of scimitar babblers well after our

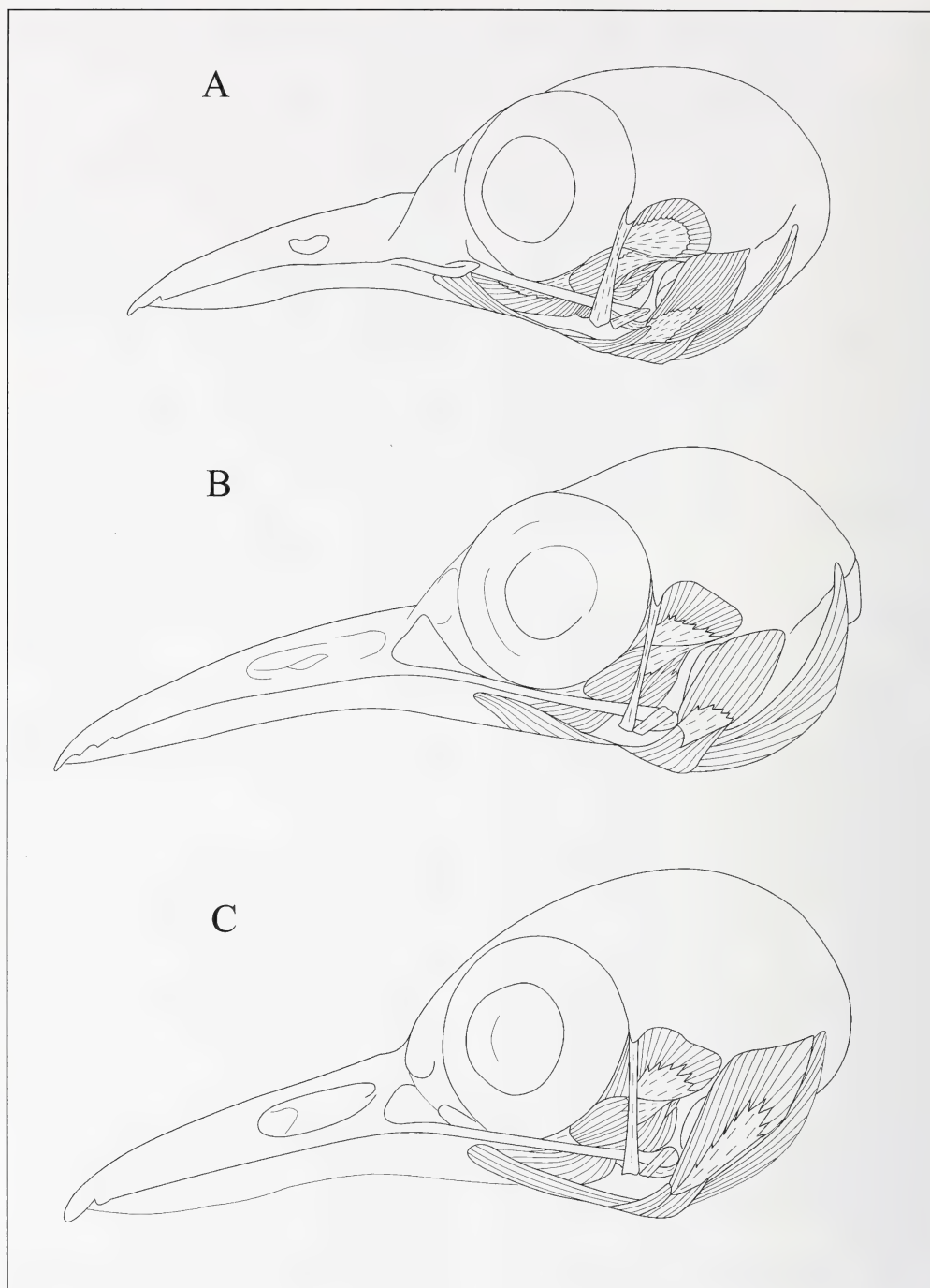


FIG. 5. Morphology of the outer layer of the jaw apparatus muscles in three insectivorous timaliid species, side view: A – Buff-breasted Babbler *Pellorneum tickelli*, B – White-bellied Yuhina *Erpornis zantholeuca*, C – Scaly-crowned Babbler *Malacopteron cinereum*.

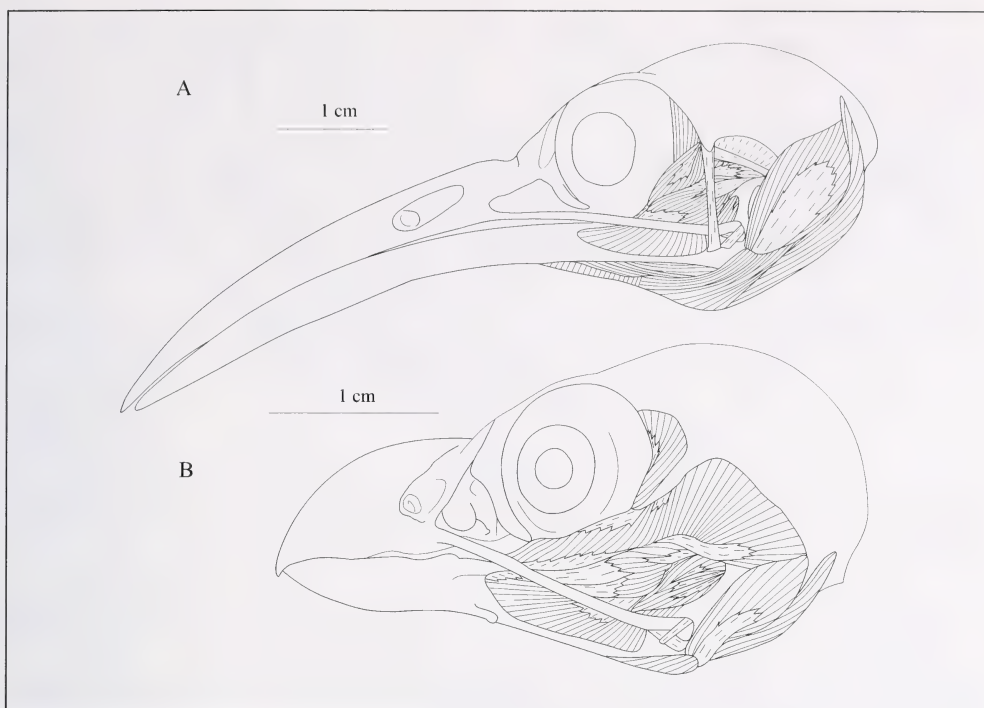


FIG. 6. Morphology of the outer layer of the jaw apparatus muscles in two insectivorous timaliid species, side view: A – Large Scimitar Babbler *Pomatorhinus hypoleucos*, B – Grey-Headed Parrotbill *Paradoxornis gularis*.

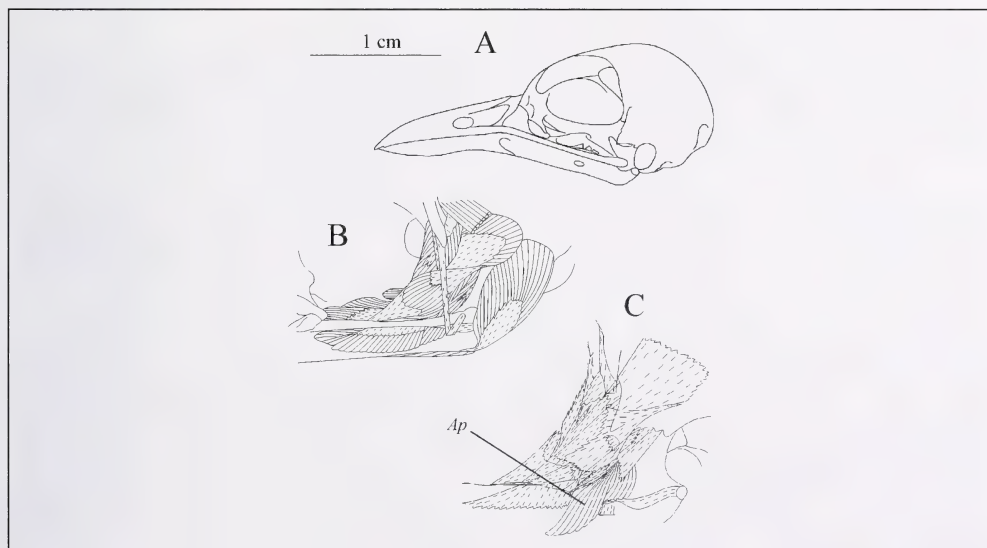


FIG. 7. Morphology of the outer layer of the jaw apparatus muscles in a frugivorous timaliid, Black-browed Fulvetta *Alcippe grotei*, side view.

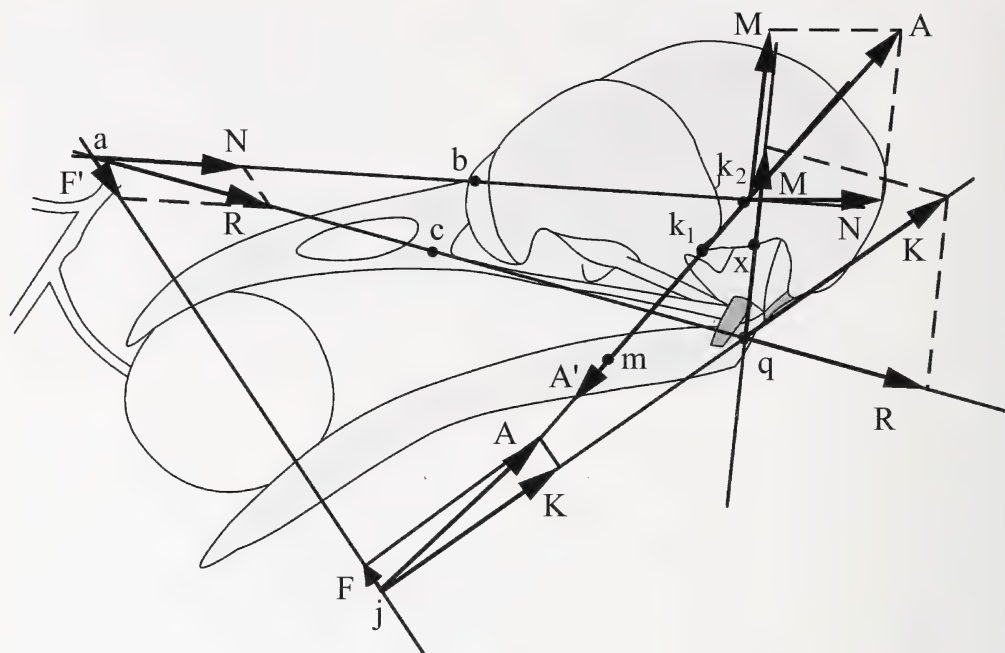


FIG. 8. Free-body diagram of forces acting in the skull during the pressure on the large food item near the tip of the bill (after Dzerzhinsky 1972 and Kalyakin 2002); the jaws are under independent muscle control. k_1 and k_2 – application points of the joint forces of adductors; for other abbreviations see Fig. 4.

morphological studies. Some trends to reinforcement are seen in laughingthrushes. However they are related to the greater body size and do not show any special features, such as higher complexity of aponeurotic carcass or additional muscular heads.

Apart from general insectivorous adaptations of the jaw apparatus, some timaliid species show certain features related to their frugivory. When the bill is widely opened the construction of the maxillary joint provides a slight dominance of the upper jaw over the lower, as has also been described in bulbuls (Kalyakin 2002; Fig. 8). This is an adaptation for an additional pressure of the upper jaw on the fruit picked from the branch. My studies of middle-sized frugivorous passerines, including 16 species of Asian Pycnonotidae, Hill Myna, and Irena (Kalyakin & Dzerzhinsky 1997; Kalyakin 1998, 2002, 2003, 2008), have shown that this reinforcement of the upper jaw in larger birds is sufficient to pick fruit from the branch. However, in the majority of studied timaliid species, *m. retractor palatini* (a very effective

retractor of the upper jaw, as only one portion of *m. pterygoideus* has direct contact with the upper jaw and the skull) and some other morphological features related to fruit-picking are not well developed. For these birds we can identify an independent action of muscles controlling the upper and lower jaws (Dzerzhinsky 1997). A well-developed set of fruit-picking adaptations was found only in Black-browed Fulvetta. The special structure of the maxillary joint is accompanied by the reduction of the tongue muscles. The absence of an anterior part of *m. brachyomandibularis* allows the processing of relatively large food items, namely fruits, at the expense of the ability to manipulate small objects, characteristic of insectivorous birds. An extremely enlarged *m. adductor caudalis* greatly adds to the retraction of the upper jaw.

Besides the morphological and functional features common to all studied timaliid species, we found some specificity in the jaw apparatus of selected species that adds some details to characteristics of their trophic adaptations (Table 2).

TABLE 2. Results of study of Southern Vietnam forest timaliid species jaw apparatus and foraging.

Species	Results of dissection	Conclusion about foraging
White-bellied Yuhina <i>Erpornis zantholeuca</i>	Quite different from other studied species by general structure, list of muscle portions, abundance of aponeuroses; clearly adopted to gaping (opening beak probing in substrate).	Insectivorous, but on different morphological base; gaping was not observed, but could be using for excavating of food from any substrate, possibly including flowers or buds.
Black-browed Fulvetta <i>Alcippe grotei</i>	Simple aponeurotic carcasses, reinforcement of upper jaw, some reduction of tongue muscles.	Insectivorous; features of adaptation to frugivory are very clear due to small body size.
Great Scimitar Babbler <i>Pomatorhinus hypoleucos</i>	General structure and composition of muscle portions common are for timaliid species, but volume of muscles are quite more then usual.	Insectivorous with strong reinforcement for probing and extraction of insects from different shelves.
Striped Tit Babbler <i>Macronous gularis</i>	Dissection wasn't done.	Probably similar with Grey-faced Tit Babbler
Grey-faced Tit Babbler <i>Macronous kelleyi</i>	Structure and composition of jaw muscles are typical for studied timaliid species, possible are not far from ancestral ones.	Typical insectivorous with orientation on collating of slowly moved or immobile food including examination of cocoons, dry leaves, etc. There are no special signs of adaptation in frugivory.
Buff-breasted Babbler <i>Pellorneum tickelli</i>	Only outer layers of muscles were described. Typical picture, wide and strong ligamentum postorbitale helps to open and slum beak quickly.	Typical insectivorous, may be with some tendency to catch mobile insects in dense vegetation more frequently then other timaliid species.
Puff-throated Babbler <i>Pellorneum ruficeps</i>	Also outer layers of muscles were examined. No special features were found besides common for other timaliid species.	Typical insectivorous, probably simple collating of insects in style common for small timaliid species.
Scaly-crowned Babbler <i>Malacopteron cinereum</i>	Full description of jaw apparatus was done, typical variant of its structure, composition and function was verified.	Typical insectivorous, collating of insects in style common for small timaliid species, no special features shown on orientation on flycatching were found.
White-crested Laughingthrush <i>Garrulax leucolophus</i>	Structure and composition of jaw muscles are typical for studied timaliid species, some degree of reinforcement of jaw apparatus is reached due to big body size.	Typical insectivorous, big food items and small fruits are accessible due to general increase of sizes of bird and its jaw apparatus.
Lesser Necklaced Laughingthrush <i>Garrulax monileger</i>	Dissection wasn't done.	Probably similar with Grey-faced Tit Babbler

DISCUSSION

The basic morphology of the jaw apparatus, and comparisons with closely-related species, indicate that timaliids are initially adapted to manipulate the substrate or food objects, having prerequisites for fruit processing. The latter ability was used to various degrees by several montane groups, but most of the family members became adapted to insectivory. The type of insectivory used by most timaliids is not a

simple collecting of abundant and easily-spotted insects, as in several Muscicapidae, Sylviidae, and some Turdidae. Timaliid insectivory involves intensive searching and excavating of slow-moving invertebrates or immobile arthropods hidden in the foraging substrate or ephemeral shelters. Field observations show that clusters of dry leaves, cocoons and pupae of insects hiding in rotten branches and bamboo stems are among the most attractive items for timaliids. This sort of basic adaptation is in good

agreement with one idea of the origin of this group in high-elevation, montane regions with relatively long cold periods, when most arthropods are inactive (Kalyakin 2006b, 2007a). Proceeding from the modern biogeography of Timaliidae, they could have evolved in the Himalayas (Collar & Robson 2007).

Our conclusions regarding the origins of the morphological features of the timaliid jaw apparatus are well supported by field observations. Timaliids are indeed specialists in terms of intensive scrutiny of various kinds of substrates, and in the capture of immobile or slow-moving arthropods. No timaliid is specialized in the catching of flying insects, despite their great abundance in lowland tropical forests. They do not even capture flying termites, a very attractive food in tropical forest for a variety of other birds from swifts to hornbills (Stepanyan 1996; our observations).

CONCLUSIONS

Most of the timaliid species from the lowland forests of southern Vietnam, including species of the genera *Malacopteron*, *Macronous*, *Pellorneum*, and *Erpornis zantholeuca*, form a guild of insectivorous birds, which likely has never used small fruits as a principal dietary item, like (e.g.) the Striped Tit Babbler. Birds of this guild, together with several other groups of Timaliidae, probably represent an early stage in the colonization by the family of lowland ecosystems. They have lost or never possessed frugivory as a foraging focus, and occupy niches as hunters of slow-moving or immobile arthropods that depend upon crypsis or hiding to avoid predators. Some of these timaliids, such as the Scaly-crowned Babbler, show initial trends to hunting active insects, including flying ones. Slowly moving timaliids in the process of scrutinizing the substrate in search of arthropods are good companions for flycatching birds, such as the Racket-tail Drongo *Dicrurus paradiseus* (King & Rappole 2001). Insects, flushed by timaliids, become the prey of a number of other avian species, perhaps resulting in the formation of mixed-species flocks in which some members capitalize on the foraging activities of others.

Several timaliid species, occupying various strata of the forest and its borders, are good runners and climbers, but not flycatchers. They have long powerful legs, well adapted for acrobatic types of movement in branches in a search of food, using visual control at a short distance. Two lineages of timaliids have species that appear partially adapted to frugivory, e.g.,

the Black-browed Fulvetta, a member of the genera or subgenera of mountain grey-headed fulvettas, and the Large Scimitar Babbler, adapted to searching in different substrates. Larger species, such as laughingthrushes, are also historically connected to montane habitats. Species of *Garrulax* that later occupied lowland forests retained the prerequisites for frugivory and, due to their larger size and powerful jaw apparatus, also for carnivory.

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